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Ryan M. Maher  
*Iowa State University*

Heidi Asbjornsen  
*Iowa State University, hasbjorn@iastate.edu*

Randall K. Kolka  
*United States Department of Agriculture*

Cynthia A. Cambardella  
*United States Department of Agriculture, cindy.cambardella@ars.usda.gov*

James W. Raich  
*Iowa State University, jraich@iastate.edu*

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## Abstract

Close relationships among climatic factors and soil respiration ( $R_s$ ) are commonly reported. However, variation in  $R_s$  across the landscape is compounded by site-specific differences that impede the development of spatially explicit models. Among factors that influence  $R_s$ , the effect of ecosystem age is poorly documented. We hypothesized that  $R_s$  increases with grassland age and tested this hypothesis in a chronosequence of tallgrass prairie reconstructions in central Iowa, U.S.A. We also assessed changes in root biomass, root ingrowth, aboveground net primary productivity (ANPP), and the strength of soil temperature and moisture in predicting  $R_s$ . We found a significant increase in total growing season  $R_s$  with prairie age ( $R^2 = 0.79$ ), ranging from 714 g C m<sup>-2</sup> in the youngest reconstruction (age 4) to 939 g C m<sup>-2</sup> in the oldest prairie (age 12). Soil temperature was a strong predictor of intra-seasonal  $R_s$  among prairies ( $R^2 = 0.78-0.87$ ) but mean growing season soil temperature and moisture did not relate to total  $R_s$ . The increase in  $R_s$  with age was positively correlated with root biomass ( $r = 0.80$ ) and ANPP ( $r = 0.87$ ) but not with root ingrowth. Our findings suggest that growing season  $R_s$  increases with tallgrass prairie age, root biomass, and ANPP during young grassland development.

## Keywords

Soil respiration, Tallgrass prairie, Grassland age, Root biomass, Belowground carbon, Aboveground production

## Disciplines

Ecology and Evolutionary Biology | Soil Science | Terrestrial and Aquatic Ecology

## Comments

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Short communication

## Changes in soil respiration across a chronosequence of tallgrass prairie reconstructions

Ryan M. Maher<sup>a,\*</sup>, Heidi Asbjornsen<sup>a</sup>, Randall K. Kolka<sup>b</sup>, Cynthia A. Cambardella<sup>c</sup>, James W. Raich<sup>d</sup>

<sup>a</sup> Department of Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, IA 50011, USA

<sup>b</sup> USDA Forest Service, Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 55744, USA

<sup>c</sup> USDA-Agricultural Research Service, National Laboratory for Agriculture and the Environment, 2110 University Boulevard, Ames, IA 50011, USA

<sup>d</sup> Department of Ecology, Evolution, and Organismal Biology, Iowa State University, 253 Bessey Hall, Ames, IA 50011, USA

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### ABSTRACT

Close relationships among climatic factors and soil respiration ( $R_s$ ) are commonly reported. However, variation in  $R_s$  across the landscape is compounded by site-specific differences that impede the development of spatially explicit models. Among factors that influence  $R_s$ , the effect of ecosystem age is poorly documented. We hypothesized that  $R_s$  increases with grassland age and tested this hypothesis in a chronosequence of tallgrass prairie reconstructions in central Iowa, U.S.A. We also assessed changes in root biomass, root ingrowth, aboveground net primary productivity (ANPP), and the strength of soil temperature and moisture in predicting  $R_s$ . We found a significant increase in total growing season  $R_s$  with prairie age ( $R^2 = 0.79$ ), ranging from 714 g C m<sup>-2</sup> in the youngest reconstruction (age 4) to 939 g C m<sup>-2</sup> in the oldest prairie (age 12). Soil temperature was a strong predictor of intra-seasonal  $R_s$  among prairies ( $R^2 = 0.78$ – $0.87$ ) but mean growing season soil temperature and moisture did not relate to total  $R_s$ . The increase in  $R_s$  with age was positively correlated with root biomass ( $r = 0.80$ ) and ANPP ( $r = 0.87$ ) but not with root ingrowth. Our findings suggest that growing season  $R_s$  increases with tallgrass prairie age, root biomass, and ANPP during young grassland development.

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### 1. Introduction

Land use change through agricultural conversion dramatically alters carbon (C) cycling processes within terrestrial ecosystems (Paustian et al., 1998). In the Midwestern U.S.A., agriculture has driven widespread conversion of tallgrass prairie ecosystems to annual cropping systems. There is growing interest in the planting and active management of perennial grasslands across these agricultural landscapes as a means to reconstruct soil C storage functions associated with native tallgrass prairie ecosystems (e.g., Kucharik et al., 2001). However, site-level variation among grasslands in former croplands complicates our ability to predict the effects of grassland reconstructions on soil processes. A greater understanding of the effects of grassland age on belowground C cycling will improve our ability to model soil C dynamics across these landscapes.

Soil respiration ( $R_s$ ), a measure of total soil metabolism that includes rhizosphere and microbial respiration, is a significant C flux that is likely altered with grassland reconstruction. Within

native tallgrass prairie ecosystems,  $R_s$  has been shown to account for a majority of total ecosystem respiration (Ham et al., 1995) and within tallgrass reconstructions, Brye et al. (2002) suggested that the ecosystem C balance could be more sensitive to fluctuations in  $R_s$  than net primary production. Despite the significance of  $R_s$  in grassland C cycling, we have a limited understanding of the magnitude and directional change in  $R_s$  over time during grassland development (Brye and Riley, 2009).

Grassland chronosequences within former cropland have documented an increase in belowground plant C with grassland development (Baer et al., 2002; Camill et al., 2004). The accumulation of plant root biomass with early grassland development may lead to an increase in soil metabolism (Odum, 1969). The estimated contribution of root respiration to total  $R_s$  in tallgrass prairie may be as high as 40% (Craine et al., 1999; Kucera and Kirkham, 1971) and root-derived detritus provides the primary substrate for microbial decomposition. In addition, both microbial biomass (Allison et al., 2005) and potential C mineralization rates (Camill et al., 2004; Baer et al., 2002) have shown to increase with young tallgrass prairie development. However, changes in soil microclimate conditions with reconstruction development could potentially confound the effects of plant root activity on soil respiration and few grassland chronosequence studies have quantified these changes (Guzman and Al-Kaisi, 2010).

\* Corresponding author at: USDA-Agricultural Research Service, 1991 Upper Buford Circle, St. Paul, MN 55108, USA. Tel.: +1 612 625 4242; fax: +1 651 649 5058.  
E-mail address: [rmaher11@gmail.com](mailto:rmaher11@gmail.com) (R.M. Maher).

This study used an 8 yr chronosequence of tallgrass prairie reconstructions to test the following hypotheses: (1) total growing season  $R_s$  will increase with tallgrass prairie age; (2) an increase in total growing season  $R_s$  with age is related to greater soil moisture availability within older reconstructions; and (3) total growing season  $R_s$  will be positively correlated with root biomass, root ingrowth, and aboveground net primary productivity (ANPP).

## 2. Materials and methods

### 2.1. Site description

This study was conducted in 2006 at the Neal Smith National Wildlife Refuge (NSNWR) in Jasper County, central Iowa (41°33' N, 93°17' W), USA. This region has a mean annual precipitation of 87.4 cm and mean annual temperature of 9.6 °C (1971–2000; MRCC, 2007). In 2006, annual precipitation was approximately 64.2 cm and average monthly temperature was 10.8 °C (NESDIS, 2007).

This study used five tallgrass prairie plantings, ranging in size from 2 to 7.5 ha, to represent a gradient in time of reconstructions that included prairies planted into formerly cropped lands in 2002 (age 4), 2000 (age 6), 1998 (age 8), 1997 (age 9), and 1994 (age 12). Prairie plantings were seeded in the late fall after a soybean crop, with seed sources shifting from local prairie remnants and outside suppliers (pre-1996) to bulk harvests from within-refuge plantings (post-1996). We also used a no-till soybean field as a reference site, planted day-of-year (DOY) 127 and harvested DOY 272, to represent a common annual crop in the region.

These plantings complement a long-term assessment of changes in soil C with tallgrass prairie establishment at NSNWR (Cambardella et al., 2004). All plantings were located on similar soil types (Mollisols; Fine-silty, mixed, superactive, mesic Typic Argiudoll and Fine, smectitic, mesic Oxyaquic Argiudoll). Similarity in specific soil characteristics analyzed in previous work (Cambardella et al., 2004) suggests that site comparisons are reasonable. Across sites, mean soil texture ranged from 2 to 3% sand, 66 to 68% silt, and 29 to 32% clay. Mean soil C ranged from 2.5% to 3.6% and soil nitrogen (N) from 0.24% to 0.32% in the top 30 cm. All sites received a prescribed burn in the fall of 2004 and therefore time since last burn remained constant. This prairie chronosequence is subject to the limitations of space-for-time substitution (Pickett, 1989); however, consideration of soil characteristics and management history in site selection, as stated above, can minimize confounding factors that influence trends due to time.

### 2.2. Soil respiration

Soil surface CO<sub>2</sub> efflux was measured with a custom, infrared gas analyzer (IRGA, LI-COR 820). Plastic (PVC) collars, 8 cm tall × 25 cm diameter (506.7 cm<sup>2</sup> soil surface area), were permanently installed one week prior to the first sampling period to minimize the effects of disturbance (Davidson et al., 2002). Collars ( $n = 10$  per site) were inserted to a depth of 2 cm and included surface litter and plant crowns, accounting for their potential high flux (Craine et al., 1999). Standing live vegetation within each collar was clipped at the soil surface 24 h before sampling.

Measurements of  $R_s$  were conducted from DOY 109 through DOY 321, approximately biweekly ( $n = 15$ ). The order in which sites were sampled was randomized for each measurement period and measurements were taken between the hours of 1000 and 1500. Soil respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) during this time period was used to represent the daily average  $R_s$  (Knapp et al., 1998; Kaye et al., 2005). Based on diurnal measurements conducted on DOY 173 and DOY 306,  $R_s$  rates between 1000 and 1500 were within 8% of the daily average. Soil temperature (10 cm) was measured simul-

taneously with  $R_s$  and volumetric soil moisture content (% water volume in 75 cm<sup>3</sup> soil; 0–6 cm) was measured with a ThetaProbe (Delta-T Devices Inc.) at four locations after each  $R_s$  measurement.

### 2.3. Scaling $R_s$ to total growing season estimates

Daily average  $R_s$  measurements were used to estimate total growing season  $R_s$  based on linear interpolation between measurement periods. This estimate assumes that a two-week measurement interval is sufficient to capture intra-seasonal variation in  $R_s$ . We tested this assumption for DOY 165 through DOY 294 using continuous soil temperature data (10 cm) collected at a nearby upland prairie site (T. Sauer, unpublished). Daily soil temperature averages were correlated with instantaneous temperature measurements for overlapping days ( $n = 9$ ) and the resulting regression models ( $R^2 = 0.81–0.97$ ) used to derive daily estimates of soil temperature. Extrapolated soil temperatures were then applied to regression models based on instantaneous  $R_s$  and soil temperature for each site using all sampling dates to estimate daily  $R_s$  for all days between DOY 165 and DOY 294. Across all prairie sites, growing season  $R_s$  totals based on instantaneous measurements alone were within 5% of the estimate based on continuous soil temperature data, lending confidence that linear interpolation provided a reasonable estimate of total growing season  $R_s$ .

### 2.4. Root biomass

Standing root biomass ( $\leq 2$  mm; live and dead combined) was sampled in the spring on DOY 100. One root core (diameter 7.0 cm; depth 30 cm) was taken in close proximity to each  $R_s$  collar within each site ( $n = 60$ ). Samples were washed using a hydropneumatic elutriation system (Russell et al., 2004), dried at 65 °C for 24 h, and sorted from organic debris. Total C and N in root biomass were determined with a LECO TruSpec CHN Analyzer.

### 2.5. Root ingrowth

Root production was estimated using the root ingrowth technique (Russell et al., 2004). For site installation, litter was removed from the soil surface and one soil core (diameter 7 cm) was harvested in close proximity to each  $R_s$  collar. The soil core was then replaced with a soil-filled root ingrowth tube and covered with surface litter. Root ingrowth tubes were constructed of polypropylene mesh tubes (16-mm<sup>2</sup> holes; Industrial Netting, Minneapolis, MN, <http://www.industrialnetting.com>), 7 cm in diameter and 30 cm in length, and sewn with mesh bottoms. Each ingrowth tube was filled with soil collected on site and sieved (6 mm) to remove roots. Ingrowth samples were washed, dried, sorted, and analyzed for total C and N.

Root ingrowth was measured for approximately three months during three overlapping time intervals: DOY 100–193 (spring), DOY 157–251 (summer), and DOY 221–310 (fall). Root ingrowth during overlapping periods, approximately 30 days, was determined based on the average daily production of overlapping ingrowth samplings. Total growing season root ingrowth ( $\text{g C m}^{-2} \text{ yr}^{-1}$ ) was estimated by multiplying the average daily growth by the number of days within each period and then summing all ingrowth periods.

### 2.6. Aboveground production

Aboveground biomass was harvested four times, on DOY 134, 178, 226, and 293. A total of eight 0.25 m<sup>2</sup> quadrats were sampled from each site. All vegetation within the quadrat was clipped, removed, and separated into live and dead fractions. Biomass was dried at 65 °C for 48 h and weighed. Aboveground net primary

**Table 1**

Changes in root biomass, root ingrowth, aboveground net primary production (ANPP), and total growing season soil respiration ( $R_s$ ) carbon (C) with age of tallgrass prairie reconstruction.

Reconstruction Age (yr)	Root biomass (g C m <sup>-2</sup> )	Root ingrowth (g C m <sup>-2</sup> yr <sup>-1</sup> )	ANPP (g C m <sup>-2</sup> yr <sup>-1</sup> )	Growing season $R_s$ (g C m <sup>-2</sup> )
4	38	89	148	714
6	131	100	271	757
8	164	202	175	747
9	186	166	368	910
12	205	176	312	939
$R^2$	0.85			0.79
$P$ -value	0.025	0.13	0.23	0.045
Soybean	17	60	336	624

The soybean crop is presented for comparison only. Coefficients of determination are reported for significant ( $P < 0.05$ ) regressions only; root biomass ( $y = -11.4 + 20.0x$ ) and growing season  $R_s$  ( $y = 578 + 30.1x$ ). Values represent site means ( $n = 8-10$ ).

production (ANPP; g m<sup>-2</sup> yr<sup>-1</sup>) was based on the sum of positive increments in live and dead biomass (Dornbush and Raich, 2006). Aboveground biomass in the soybean crop was estimated based on peak live biomass (DOY 244). Aboveground biomass in all ages was converted to grams of C based on an estimate of 43% C in plant biomass (Kucharik et al., 2006).

### 2.7. Statistical analysis

Statistical analyses were conducted using JMP 6.0 (SAS Institute Inc.). Soil respiration was natural log-transformed prior to analyses to meet assumptions of uniform variance. Linear regression was used to model the effect of temperature on  $R_s$  within each location for each age (Boone et al., 1998). Multiple regression models, including both soil temperature, soil moisture, and the interaction term, were used to assess the importance of soil moisture in explaining  $R_s$ . We also assessed changes in mean growing season soil temperature and moisture with prairie age using linear regression and used correlation analyses to test the relationship with total growing season  $R_s$  ( $n = 5$ ;  $P < 0.05$ ).

Significant changes in total growing season  $R_s$ , root biomass, root ingrowth, and ANPP C with time since prairie reconstruction were examined using linear regression with site means ( $n = 5$ ;  $P < 0.05$ ). The soybean crop is included for comparison only and is not included in linear regressions. We used correlation analyses to assess significant relationships ( $P < 0.05$ ) between total growing season  $R_s$ , root biomass, root ingrowth, and ANPP C among ages ( $n = 5$ ).

## 3. Results

### 3.1. Soil temperature, soil moisture, and $R_s$

Mean growing season soil temperatures showed no trend with prairie age ( $P = 0.59$ ) and ranged from 16.9°C to 17.9°C with maximum temperatures (24.5°C to 26.4°C) reached between DOY 194 and 226 (data not shown). Mean soil moisture ranged from 27.6% to 31.0% with minimums reached between DOY 166 and 215 (15.9–19.4%) and did not show a trend with age ( $P = 0.24$ ). Similar to soil temperature,  $R_s$  peaked within each age between DOY 194 and 215, with maximum mean daily  $R_s$  ranging from 6.20 (age 4) to 8.32 (age 9) g C m<sup>-2</sup> day<sup>-1</sup>. Coefficients of variation (CV) in  $R_s$  on a given sampling date averaged 21% with a range from 14% to 33% across sites, consistent with others using similar chambers (Davidson et al., 2002).

Intra-seasonal changes in  $R_s$  were strongly related to soil temperature within each prairie age ( $P < 0.0001$ ; models not shown). Soil temperature-based regression models explained from 78% (age 4) to 87% (age 8) of the variation in  $R_s$ . The addition of soil moisture to soil temperature-based models explained a significant amount

of intra-seasonal  $R_s$  variation within each age (from  $P < 0.0001$  to  $P < 0.02$ ); however, moisture added limited explanatory power and the improvement in model  $R^2$  was greatest in the 4 yr old prairie (from  $R^2 = 0.78$  to 0.87). The temperature by moisture interaction term was only significant for the 4, 8, and 12 yr old prairies (from  $P < 0.0003$  to  $P < 0.059$ ) but added no predictive power.

### 3.2. Changes in total growing season $R_s$ and plant growth with prairie age

Total growing season  $R_s$  showed a significant, positive increase with tallgrass prairie age ( $R^2 = 0.79$ ,  $P < 0.045$ ), ranging from 714 (age 4) to 939 (age 12) g C m<sup>-2</sup> (Table 1). Cumulative  $R_s$  showed that the two oldest prairies (ages 9 and 12) accelerated at a greater rate into the mid-summer months in comparison to the other prairies (ages 4, 6, and 8) (Fig. 1a). Root biomass C also showed a significant linear increase with prairie age ( $R^2 = 0.85$ ,  $P < 0.025$ ) and root ingrowth C increased with prairie age, although this trend was not statistically significant ( $P = 0.13$ ; Table 1). Cumulative root ingrowth among prairie ages showed greater spring and summer ingrowth rates in the 8, 9, and 12 yr old prairies relative to ages 4 and 6 (Fig. 1b). Aboveground NPP C showed no significant linear trend with prairie age ( $P = 0.23$ ; Table 1). In comparison, the soybean crop had the lowest root biomass and ingrowth, less total  $R_s$ , and ANPP similar to the oldest prairies (Table 1).

### 3.3. Correlations among total growing season $R_s$ , soil microclimate, and plant growth

We found no relationship between total growing season  $R_s$  and mean soil temperature ( $P = 0.70$ ) or moisture ( $P = 0.69$ ) across prairie ages. We observed a positive correlation between total growing season  $R_s$  and root biomass C ( $r = 0.80$ ,  $P = 0.11$ ; Fig. 2a), but did not find a significant correlation between total growing season  $R_s$  and root ingrowth C ( $r = 0.50$ ,  $P = 0.39$ ; Fig. 2b). However, exclusion of the 8 yr reconstruction from the analysis resulted in a significant, positive correlation between  $R_s$  and both root biomass ( $r = 0.93$ ,  $P = 0.069$ ) and root ingrowth C ( $r = 0.998$ ,  $P = 0.0018$ ). Aboveground NPP C and total growing season  $R_s$  were strongly correlated across prairie ages ( $r = 0.87$ ,  $P = 0.06$ ; Fig. 2c).

## 4. Discussion

### 4.1. Soil respiration, soil microclimate, and prairie age

Intra-seasonal variation in  $R_s$  was strongly related to changes in soil temperature across reconstructions, similar to studies in native tallgrass prairies (Knapp et al., 1998; Kucera and Kirkham, 1971; Mielnick and Dugas, 2000) and older prairie reconstructions

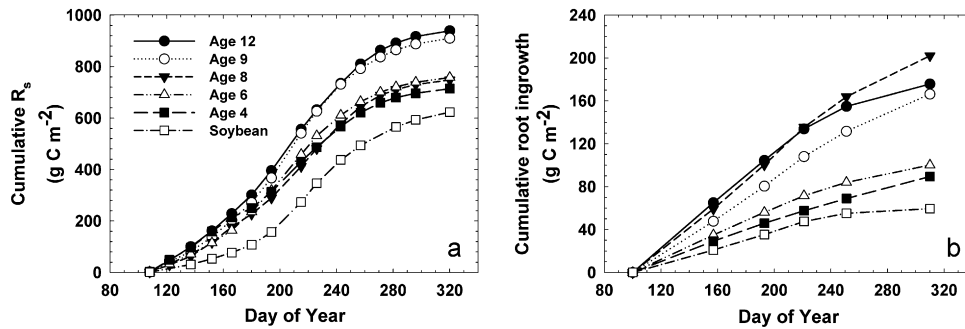


Fig. 1. Cumulative (a) soil respiration ( $R_s$ ) and (b) root ingrowth carbon (C) for five different-aged tallgrass prairie reconstructions and a soybean crop. Values shown represent site means ( $n = 10$ ).

(Kucharik et al., 2006). While low soil moisture has the potential to limit  $R_s$  and confound predictions based on soil temperature (Kucharik et al., 2006), soil moisture explained limited additional  $R_s$  variation within our reconstructed prairies. However, we found the greatest effect of soil moisture on  $R_s$  in the youngest reconstruction (age 4 yr) and soil moisture improved  $R_s$  predictions for that site. This difference in the effect of soil moisture may relate to changes in live and dead biomass among ages, where larger amounts of aboveground detritus in older reconstructions provided greater buffering capacity and thus limited soil drying and wetting (Knapp and Seastedt, 1996). Despite changes in above and belowground plant growth, there was no trend in mean growing season soil temperature or moisture with age and these abiotic controls did not relate to changes in total growing season  $R_s$ .

#### 4.2. Changes in plant growth with prairie age

We found an increase in root biomass across the chronosequence that was consistent with the establishment and accumulation of perennial roots with tallgrass prairie development (Brye et al., 2002). We observed a threefold increase in root biomass and a twofold increase in root C:N (data not shown) between the 4 and 6 yr old prairies. While the trend toward increasing root ingrowth with prairie age was less predictable, we found higher root ingrowth rates among reconstructions  $\geq$  age 8 and a stronger increase in C:N during the summer period compared to the younger reconstructions (data not shown). A shift toward  $C_4$  grass dominance in older plantings (Camill et al., 2004; Jastrow, 1987), with greater belowground biomass and higher N use efficiency (Craine et al., 2002), may account for the observed increases in belowground plant C cycling within older reconstructions.

We found no consistent trend in ANPP with prairie age and no tradeoff between ANPP and root ingrowth across the chronosequence. For example, both ANPP and root ingrowth in the oldest

reconstruction were approximately double that of the youngest prairie. Others measuring both above and belowground plant C in tallgrass prairies have documented an increase in belowground production without similar changes in aboveground production (Brye and Riley, 2009; Camill et al., 2004).

#### 4.3. Total growing season $R_s$ , plant growth, and prairie age

Our results indicated that total growing season  $R_s$  increased 32% over the 8 yr chronosequence. Guzman and Al-Kaisi (2010) also found an increase in cumulative  $R_s$  among tallgrass prairie reconstructions (ages 3, 8, and 13) while Brye and Riley (2009) found no difference in seasonal  $R_s$  rates in a prairie chronosequence (ages 3, 4, 5 and 26 yr) in the south-central USA. The latter grasslands were located in a warmer, humid-temperate climate and established in former pasture, conditions that likely led to greater initial heterotrophic activity, reduced the seasonality of  $R_s$ , and may have limited the effect of site-level differences in root biomass. In our sites, prairies were planted into no-till soybean fields, and therefore rapid accumulation of belowground plant biomass during the early stages of reconstruction likely translated into greater rates of  $R_s$  with age.

The positive relationship between root biomass and total  $R_s$  has been found in other temperate grasslands (Craine and Wedin, 2002; Dornbush and Raich, 2006; Kucera and Kirkham, 1971), but it has not been well documented along a gradient of grassland reconstruction age and few studies have estimated root ingrowth in combination with  $R_s$  in young grasslands. While we expected a strong correlation between total growing season  $R_s$  and root ingrowth, our results from the anomalous 8 yr old reconstruction affected an otherwise highly significant, positive relationship. This result could be an artifact of site-specific conditions or historical management and we recognize the limitation of this chronosequence in the absence of replicated plantings and/or multiple years

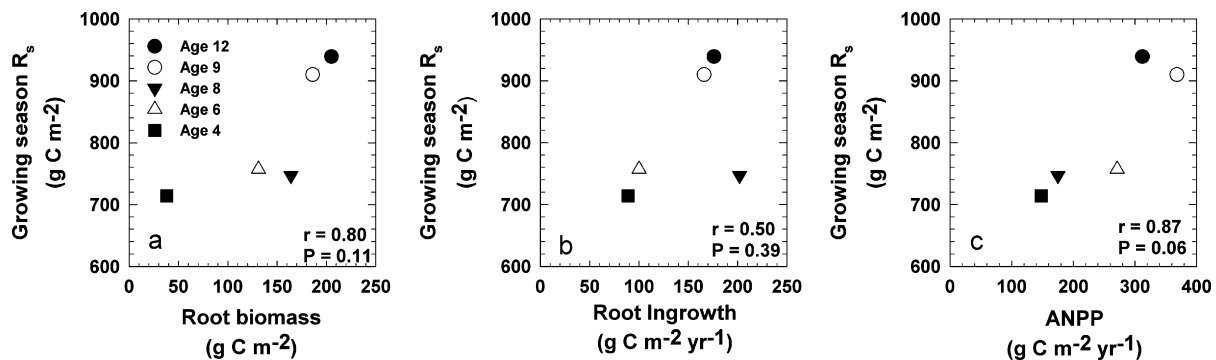


Fig. 2. Correlations between total growing season soil respiration ( $R_s$ ) and (a) root biomass, (b) root ingrowth, and (c) aboveground net primary production (ANPP) carbon (C) for five-different aged tallgrass prairie reconstructions. Values shown represent site means ( $n = 8-10$ ).

of data. Nevertheless, our chronosequence did elucidate strong trends in  $R_s$ .

A positive relationship between growing season  $R_s$  and root biomass may be attributed to greater microbial activity and/or increases in root respiration associated with greater root growth in older prairies. While total  $R_s$  increased by one-third across the chronosequence, we found a fivefold increase in root biomass and a twofold increase in root ingrowth. In the 4 yr old prairie,  $CO_2$  produced per gram of root tissue was more similar to a soybean crop and over 4 times greater than the oldest prairies. These trends may indicate a greater percentage of heterotrophic  $R_s$  in the youngest sites with rates leveling off in older reconstructions.

A strong positive correlation between total growing season  $R_s$  and ANPP is in contrast to Dornbush and Raich (2006) and consistent with others that have found a relationship between canopy characteristics and  $R_s$  (Bremer and Ham, 2002; Craine et al., 1999). Aboveground productivity may serve as a measure of belowground C supply (Bremer et al., 1998) and greater productivity in older reconstructions may help explain an increase in  $R_s$  across young grasslands. Our inability to distinguish the importance of root biomass and aboveground production as predictors of  $R_s$  suggests the importance of additional work over multiple years that investigates the drivers of increasing rates of  $R_s$  with young grassland development.

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